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SOME FEATURES OF THE ANATOMY OF THE FOLIAR BUNDLE[1]

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(WITH PLATE XVII)

Although the vascular system of the leaf in the Cycadaceae has for some time been recognized as a region where primitive structures, notably centripetal wood, have persisted longer than anywhere else in the plant, the general principle of the conservatism of the foliar organ has only recently been more widely extended and found to hold good for all the main groups of vascular plants: Lycopsida, Filicales, Gymnosperms, and Angiosperms. The position of the protoxylem in relation to the later formed elements of the wood is very constant in the large orders, but its importance in determining phylogenetic relationships seems often to have been overlooked. A brief summary of the structure of the leaf trace and foliar conducting system of all families of vascular plants, with special reference to the position of the protoxylem, and a more particular account of conditions in the living Cycadaceae, the only existing gymnosperms with centripetal wood, together with a discussion of the bearing of the results on our views as to the evolutionary history of the higher plants, is the purpose of the present paper.

That the base of the leaf trace, since it is least subject to changes in external conditions, should retain ancestral structures longer than does any other portion of the foliar system seems logical, and this has been proven to be true in several groups of vascular plants. It is therefore in this region that we should look for the primitive structure of the foliar bundle.

In all the Lycopsida where the anatomy of the leaf is known (*Equisetum*, *Lycopodium*, *Selaginella*, *Phylloglossum*, *Tmesipteris*, *Psilotum*, *Isoetes*, *Lepidodendron*, and *Sigillaria*), the vascular strand at the base, and in the majority of instances throughout the lamina, of the leaf, is a single concentric strand, roughly circular in cross-section, and with one median mesarch[2] protoxylem group. This condition also occurs at the base of the leaf trace in the Osmundaceae and Ophioglossaceae, and it apparently is present at the node of the Botryopterideae (1), and therefore seems to have been the primitive one for these families. It is very evidently the earliest type of foliar strand in vascular plants, and has persisted almost unchanged in the microphyllous Lycopsida, but in the megaphyllous Pteropsida has undergone extreme modification.

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[1] Contribution from the Phanerogamic Laboratories of Harvard University, no. 33.

A very ancient type of leaf bundle has recently been investigated by BERTRAND in his account of the anatomy of the leaf in the Zygopterideae (1), one of the three families of the Botryopterideae, those simple protostelic ferns which clearly stand close to the ancestors of the modern Filicales. The early condition of the leaf trace in this group is of importance as representing the primitive one for all ferns. This has been found by BERTRAND in the simpler forms of the Zygopterideae, such as *Clepsydropsis* and *Asterochlaena*. These genera possess a leaf bundle which is concentric and rather elliptical in shape, and which contains at either end an island of parenchyma imbedded in the xylem. Around the island are placed the protoxylem elements, which are irregularly scattered in the former genus and in two distinct groups in the latter. BERTRAND has established a very complete series of forms between this type of leaf strand and the more complicated bundles of the remaining Botryopterideae, all of which seem clearly to have been derived from the simple diarch and mesarch condition. The original monarch structure persists at the base of the trace.

In a recent paper (9) the writer has endeavored to show how the leaf bundle of the modern Filicales has been developed from that of these primitive Zygopterideae. Aside from the change in shape and the breaking up of the strand into separate bundles, the most notable difference between the modern forms and their ancestors

[2] The term "mesarch," as used in the present paper, is descriptive of any protoxylem group, whether situated at the axis of the stem or not, which is surrounded by metaxylem. "Endarch" describes any condition where the protoxylem is not at the axis and where there is no metaxylem (centripetal wood) formed on its inner face. "Exarch" describes any condition where all the primary metaxylem is formed on the inner or adaxial side of the protoxylem.

is in the position of the protoxylem. In the petiole of every living genus of ferns except *Lygodium*, the first-formed tracheids are endarch, and the upward development of the filicinean leaf seems to be uniformly marked by the disappearance of its centripetal wood. At the base of the leaf trace in many ferns a mesarch condition still persists. Here the protoxylem is usually simply mixed indiscriminately in the metaxylem, but in those rather rare cases where it shows a definite attachment either way, it almost always becomes continuous with the centrifugal wood. The base of the leaf trace of *Thamnopteris*, a primitive osmundaceous fern, as described by KIDSTON and GWYNNE-VAUGHAN (3), is a good example of this. Endarchy and the attachment of the protoxylem to the centrifugal wood are therefore distinctive characters of the advanced filicinean foliar bundle.

The close affinity of the Cycadofilices to the ferns is manifest in the structure of the leaf trace as well as in many other characters, and there seems good reason to believe that the foliar strand in this group of early seed plants has been derived from a bundle very similar to that of *Clepsydropsis* or *Asterochlaena*.

The most primitive genera of the Cycadofilices and those which approach the ferns most closely in all their characters are *Calamopitys*, *Lyginodendron*, and *Heterangium*. In *Calamopitys*, which is a very ancient form, going back to the Devonian, the base of the leaf trace, while still one of the bundles which surrounds the pith, is a single strand, with a cluster of protoxylem mixed with parenchyma at its center. In most species the centripetal wood becomes reduced at the very base of the bundle, and in *C. Beinertiana*, as described by SCOTT (5), it is actually broken through, the protoxylem becomes continuous with the centrifugal wood, and an endarch condition results. As the single mesarch trace leaves the stele, its protoxylem group divides into two parts, which lie near the outer face of the bundle, and each of these soon divides again into two. The trace on becoming free splits equally into two diarch, mesarch, and concentric strands, which pass out through the cortex. In the base of the petiole these split up into an arc of six bundles. The primitive monarch condition is therefore present at the very base of the trace; this soon takes on the diarch structure of *Clepsydropsis;* and this in turn assumes a tetrarch condition, the striking similarity of which to the bundle of *Asterochlaena* has been noted by BERTRAND. It is noteworthy that the typical modern fern character of endarchy is present only in the stem. In the leaf trace in the cortex, the first formed elements of the wood seem to be clearly connected with neither face of the bundle.

Conditions in *Lyginodendron* are very similar. The trace at its base is monarch, and though true endarchy apparently never occurs in this genus, the protoxylem group, which lies near the outer edge of the bundle on the abaxial side of an immersed island of parenchyma, is always continuous and in seriation with the narrow arc of centrifugal wood. This relation of the protoxylem to the metaxylem persists throughout the course of the leaf trace in the cortex, but is apparently lost in the petiolar bundle, where the earliest tracheids show no definite attachment to either the inner or the outer wood.

The single protoxylem group soon divides into two (fig. 6), as in *Calamopitys*, and the trace in a short time also separates into two equal parts, which shortly become diarch. These four clusters of protoxylem are all near the outside of the metaxylem, but are seriated with the centrifugal wood if at all. In the petiole the two strands become united by their abaxial ends into a tetrarch arch, which becomes gradually wider and more flattened and soon contains eight to ten protoxylem groups, all of which are clearly mesarch. This wide bundle often becomes divided into several distinct strands, which in the upper part of the rachis come together into a tetrarch and finally triarch and mesarch bundle, such as is figured by SCOTT in his description (**6**). It is noteworthy that in the petiole and rachis the abaxial elements are always smaller than the adaxial ones, a condition which is often found in the leaves of living ferns.

The structure of the trace in *Heterangium* is very similar to that in *Lyginodendron* except that it often remains undivided. The mesarch protoxylem here as well as in the stele is always in seriation with the centrifugal wood.

It is clear that in these three genera we have to deal with plants showing a strikingly close resemblance in the lower and more primitive portions of their leaf bundles to conditions which prevailed in the foliar strands of the early Botryopterideae, and it seems reasonable to suppose that this resemblance indicates a phylogenetic relationship between the two groups. These cycad-ferns, however, show their advanced condition by the possession of a much more complicated petiolar system, and by displaying the tendency shown by modern ferns for the protoxylem to become continuous with the centrifugal wood and to be at last completely endarch.

The remaining Cycadofilices show a very different structure in their leaf bundles. Here the progression, instead of being toward endarchy, is all toward exarchy, and the primitive mesarch trace with protoxylem near the outside loses its narrow zone of centrifugal wood, and its protoxylem becomes continuous with the centripetal wood, thus forming a direct contrast to the trace of *Lyginodendron*. The *Myeloxylon* type of bundle characteristic of the petioles of *Medullosa* and *Sutcliffia* shows clearly this exarch condition, though *Colpoxylon*, which often possesses only a single vascular cylinder in its stem and which is therefore probably more primitive than the other two genera, shows traces of centrifugal wood and the ancient mesarch structure. In all these genera the petiolar vascular system consists of a large number of bundles more or less irregularly arranged, but, in *Medullosa* at least, the base of the leaf trace is a single strand possessing one or more groups of protoxylem which seem to be slightly imbedded in the metaxylem.

In *Megaloxylon* the base of the leaf trace is the only part of the foliar strand of which the structure is known, and it is here a single exarch bundle.

Ptychoxylon Levyi, one of the Cycadoxyleae, shows a closer approach to the primitive Cycadofilices, for here the trace is a double one, each part of which, however, instead of being mesarch is clearly exarch.

In those primitive gymnosperms of the Palaeozoic included in the cordaitean alliance, we find the same exarch structure in the leaf bundle, which almost always consists at its base of two strands. In *Poroxylon* this pair of monarch bundles, which ultimately unite at their very base, are carried well down into the stele, the primary wood of which is thus entirely centripetal. In the petiole and blade of the leaf, the double trace divides into a series of parallel strands, each of which possesses a mass of exarch primary wood, on the outer side of which, except at the edges of the leaf, is a zone of secondary xylem, just as in the leaves of living cycads.

In *Mesoxylon*, a new genus recently established by SCOTT and MASLEN (**7**) to include forms intermediate between *Poroxylon* and the Cordaiteae, we see in the stem the beginnings of the endarch condition of the higher gymnosperms. The double leaf trace is still exarch, the protoxylem being in seriation with the centripetal wood which, in the very lowest part of its course, in several species, becomes much reduced and may finally disappear, leaving as the only relic of the primary wood the cluster of protoxylem, which is separated by parenchyma from the centrifugal secondary xylem. The structure of the leaf trace and foliar bundles in this genus is the same as in *Poroxylon*.

In the case of Cordaites, however, the typical stem structure of the modern gymnosperms makes its appearance, for here the protoxylem attaches itself to the centrifugal wood, which is almost, if not quite, entirely secondary. In the double leaf trace, however, well developed centripetal primary wood appears, with exarch protoxylem on its outer face. In the leaf blade the veins are clearly exarch. In certain species centrifugal xylem is present here, separated by parenchyma from the protoxylem and probably secondary in origin, but this is absent in the simpler forms such as *C. principalis*, where the structure is strikingly like that of a *Medullosa* bundle.

There are certain other fossil plants, probably rather closely related to *Poroxylon* and the Cordaiteae, which possess a somewhat similar type of leaf trace and primary wood, and which have been grouped by SCOTT under the family name of Pityeae.

In the genus *Pitys* the trace shows signs of bifurcation as it passes out, and it is clearly mesarch, as are the medullary strands of primary xylem. The bundles are all small, however, and the protoxylem shows no tendency to align itself with either the centrifugal or centripetal wood, showing in this respect a primitive condition.

Dadoxylon Spenceri shows considerable resemblance to *Poroxylon*, for its leaf trace, at first single, becomes double before leaving the stele, and possesses well developed primary centripetal wood, on the outer face of which occurs the exarch protoxylem. At the very base of the trace, however, this primary wood disappears and an endarch condition results.

It seems highly probable that the living Coniferales have been derived from plants closely related to the Cordaitales, but that, in the course of their development, the modern members of the group have almost entirely lost the centripetal primary wood so characteristic of their ancestors. In the cretaceous genus *Prepinus*, however, JEFFREY (2) has recently described an intermediate condition between ancient and living forms, for in the leaf of this primitive pine there is abundant centripetal wood. Though the protoxylem is adjacent to this, it is apparently in seriation with the centrifugal part of the bundle, which is very probably modified secondary xylem, as indicated by the presence of abortive medullary rays. In this case, apparently, the first-formed tracheids had assumed the typical coniferous position before the disappearance of the centripetal xylem. We shall find a very similar condition at the base of the petiole in living cycads.

Among the higher modern gymnosperms, the only occurrence of centripetal wood is in *Ginkgo*, where it is present as scattered tracheids, not in connection with the protoxylem, in the cotyledons, vegetative leaves, and anthers. This genus, which on other evidence is accounted one of the most primitive of the existing gymnosperms, also possesses a double leaf bundle and a wide, parallel-veined, rather cordaitean lamina.

The occurrence of a double foliar strand, in the more ancient of the living conifers, seems without much question to be the persistence of such a double trace as is found at the base of the leaf in the Cordaitales. The double foliar bundle found by Miss THOMAS (12) in the seedlings of many angiosperms is probably also an indication of a primitive condition. The leaf trace in the adult members of this group takes on a great variety of forms, and never displays the true centripetal xylem or "cryptogamic wood" of the early gymnosperms.

The mesozoic Cycadophyta, exemplified by the two genera *Cycadeoidea* and *Bennettites*, though showing in their cauline central cylinders the endarch condition characteristic of modern cycads and other gymnosperms, still possess primitive features in their leaves. The foliar trace as it departs from the stele is a single arched bundle. In the base of the petiole of *Cycadeoidea*, as observed by WIELAND (**13**), and of *Bennettites Gibsonianus*, as observed by SEWARD (**8**), there is a considerable amount of primary centripetal wood and of radially arranged secondary centrifugal wood, with protoxylem between the two. The seriation of the protoxylem is impossible to make out, but it was doubtless exarch, as in modern cycads. The centrifugal wood apparently diminished in amount in the upper part of the petiole. The structure of the vascular bundle in the lamina of the leaf is described by WIELAND in *Cycadeoidea* as "mesarch" and very similar to that in living cycads.

Certain recent discoveries by Miss STOPES and FUJII are of importance in this connection. The leaf blade of *Niponophyllum*, as described by these authors from the Cretaceous of Japan (**11**), is parallel veined and possesses collateral exarch vascular bundles with no centrifugal wood, thus presenting a very close resemblance to certain of the more simple types of leaf among the palaeozoic Cordaitales.

In *Nilssonia orientalis*, another Japanese cretaceous form described by Miss STOPES (**10**), the leaf blade is pinnate, having a strong midrib from which come off parallel lateral veins. The vascular strands here also seem to be clearly exarch, with no trace of centrifugal wood. The structure of the stele and of the leaf trace in neither of these forms is known.

The living Cycadales show a close resemblance anatomically to the palaeozoic Cycadoxyleae, notably *Ptychoxylon*. The central cylinder of the stem is always endarch with no centripetal xylem, save for a few scattered tracheids, not connected with protoxylem, in the reproductive axes of certain species. The leaf trace departs as a double bundle, the halves of which soon separate and pass around the stem in opposite directions before entering the base of the leaf, where they divide into a many-bundled arch. Very primitive structures are retained, as in so many former cases, only in the petiole and blade. The vascular anatomy of this portion of the plant, with special reference to the position of the protoxylem, was investigated by the writer in a considerable number of species.[3] The results obtained agree in general with those of METTENIUS (4) and other later investigators.

At the very base of the leaf trace in all the species the primary wood becomes increased in amount at the flanks of the bundle, and two adaxial projections are here formed which finally unite behind the original position of the protoxylem and inclose a small island of parenchyma. The protoxylem either follows one or both of these masses of metaxylem backward, always remaining attached to them, or else swings over to the centripetal wood as soon as the two arms of the latter unite. Just before this change takes place, the bundle presents a close similarity to that of the leaf of *Prepinus*, for both centripetal and centrifugal wood are well developed, and the protoxylem is in seriation with the latter (fig. 5).

The centrifugal wood becomes very rapidly diminished in amount as the bundle ascends, so that in the middle and upper portion of the petiole in many species, such as *Zamia integrifolia* and *Encephalartos Altensteinii*, it is either absent in most of the strands or represented by only two or three elements (fig. 2). It is also noteworthy that, except perhaps at the very base of the petiole, this outer xylem seems to be entirely secondary, as is shown by its relation to the phloem. All but the extreme outer part of this latter tissue is clearly secondary and radially arranged, and the centrifugal tracheids are almost always just at the inner ends of the rows of phloem elements, and seem unquestionably to have been produced by the same cambial activity (figs. 1 and 3). They are usually pitted and not scalariform, as are most of the elements of the centripetal xylem.

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[3] These include Cycas verticillata, C. media, C. celebica, C. ruminiana, C. circinalis, Zamia furfuracea, Z. macrophylla, Z. Loddegesii, Z. integrifolia, Z. Skinneri, Z. Linderi, Z. muricata, Z. Seiboldii, Ceratozamia latifolia, C. mexicana, C. kuesteriana, Encephalartos horridus, E. Altensteinii, E. Lehmanii, Microzamia spiralis, Dioon edule, and Bowenia spectabilis.

The protoxylem is always attached to the primary centripetal wood, which forms the great bulk of every bundle, and it is clearly in seriation with it, the smallest and ringed elements being on the very outside and becoming successively closely ringed, spiral, and pitted as we approach the inner or adaxial edge of the strand (fig. 4). Between the protoxylem and the centrifugal wood there is in nearly every case a row of parenchyma, one or two cells wide, just as in the cordaitean leaves which possess centrifugal wood. The petiolar bundles may vary in shape from narrowly triangular, with the protoxylem carried up on the apex, to almost semicircular, with the first formed tracheids in the middle of the flat upper side.

The resemblance of a cycad leaf bundle to the foliar trace of *Lyginodendron* has been much emphasized by SCOTT and others. There are apparently two very vital differences between the two, however, for the former has no centrifugal primary wood, as has the latter, and in the cycad leaf the protoxylem is distinctly seriated with the centripetal xylem, and not with the centrifugal, as it is in *Lyginodendron*. The one is exarch and the other mesarch with a tendency toward endarchy. Scattered bundles were observed in several species, where the protoxylem connected the inner with the outer wood, being attached to both. Such cases are doubtless reduced and due to the partial abortion of the separating zone of parenchyma. In all of them the protoxylem remained in seriation with the centripetal wood.

In the leaf blade the centrifugal secondary wood is still further reduced, especially when the bundles become small at the end of a pinna. In several species, such as *Dioon edule*, it is altogether absent, and in no case is it represented by more than three or four cells. These often lose their radial arrangement and tend to cluster round the outer face of the protoxylem cluster. This gives the mesarch appearance, which is probably similar to what WIELAND saw in the blade of *Cycadeoidea*. In the small cotyledonary traces of *Bowenia*, WORSDELL observed a true mesarch structure, which may perhaps be a reversion to the very primitive botryopteridean condition.

Conclusions

The following general phylogenetic conclusions may be drawn from a study of the leaf trace and foliar bundle of vascular plants.

The primitive foliar bundle was a single monarch and mesarch vascular strand. This has persisted in the leaf trace of all the Lycopsida and in the blade of many of them, thus furnishing further evidence of the unity of the group and of its relatively primitive position.

This type of bundle is present at the base of the leaf trace in the Osmundaceae and in certain of the Ophioglossaceae, which thus seem to have been early separated from the other ferns.

The leaf bundle of the primitive palaeozoic Filicales was a diarch and mesarch one. By the disappearance of its centripetal wood, this has given rise to the endarch foliar strands of living ferns, which have apparently been derived from the more ancient of the Botryopterideae.

The diarch and mesarch leaf bundle is also the primitive one for the seed plants, which were developed along two main lines from forms related to the early Botryopterideae, but which had acquired the seed habit. The members of the first series, including *Calamopitys*, *Lyginodendron*, and *Heterangium*, show the fern tendency for the protoxylem of the stele and leaf trace to become continuous and in seriation with the *centrifugal* wood, and for an ultimately endarch condition to result. The other series, which includes all remaining gymnosperms, and probably the angiosperms, shows in its earliest and most primitive forms the tendency in the vascular system of the stem and leaf for the protoxylem to become continuous and in seriation with the *centripetal* wood, and for an ultimately exarch condition to result.

These two groups are also clearly separated on other evidence. The endarch series are very fernlike in habit, possess seeds of a peculiar type, and show in their petiolar bundles (at least in *Lyginodendron*) that ancestral mesarch condition of the Botryopterideae where the protoxylem shows no preference for either the inner or the outer wood. The early members of the exarch group, however, such as *Medullosa*, do not show such striking resemblances to the ferns, possess seeds of a higher and more cycadean type, and display an exarch condition not only in the leaf trace but throughout the petiolar system.

The double trace is clearly present in the endarch series, and is also found in most of the exarch forms, including the higher Cycadofilices; *Poroxylon*, *Cordaites*, and their allies; many modern conifers, and the living Cycadales. It seems clearly to have been a primitive character, and to have arisen from a constriction of the single diarch strand which was present in the ancestors of all seed plants.

The endarch line of development apparently ended blindly and did not give rise to the typically endarch higher plants, which were developed along several distinct lines from a plexus of forms in the exarch group possessing a double leaf trace and seeds resembling those of *Medullosa.*

The Poroxyleae, Pityeae, and Cordaiteae came from this plexus at a very remote period. The tendency among this series has been toward the development of a parallel veined leaf, a clearly gymnospermous type of reproduction, and an endarch condition of the central cylinder, together with a wide zone of secondary wood.

The parallel venation of the leaf has doubtless been derived from a pinnate condition, with a two-bundled exarch rachis, a structure which has persisted only at the base of the trace. The cordaitean type of leaf seems to have existed in the Cretaceous, as is shown by the occurrence at that period of such forms as *Niponophyllum.* The genus *Nilssonia*, possessing a simple leaf with a distinct midrib but with clearly parallel lateral veins, shows an intermediate condition between a pinnate cycadean leaf and a parallel veined condition, and gives a suggestion as to how the latter may have been produced.

The cordaitean type of reproduction is unknown in the Cycadofilices, but *Trigonocarpon*, the seed of *Medullosa*, approaches closely the seeds of the Cordaiteae.

The endarch condition of the central cylinder has been caused by the disappearance of the centripetal primary wood of an exarch stem consequent upon the great increase in bulk of the centrifugal secondary wood, to which the protoxylem has finally attached itself.

A second line from the double-bundled *Medullosa*-like plexus of the exarch group, but one which lies close to the cordaitean alliance, has given rise to the Ginkgoales, the Coniferales, and probably the angiosperms. Centripetal wood persists here only in *Ginkgo*, and in the leaves of such ancient conifers as *Prepinus*. Endarchy is apparently elsewhere universal, although our knowledge of conditions in the earlier forms is very slight. *Ginkgo* and the more primitive conifers possess a double foliar bundle, and all members of both groups have parallel veined leaves. The double bundle also appears in seedlings of certain angiosperms, but this series has otherwise departed very widely from its palaeozoic ancestry.

A third line from our ancient stock gave rise to the cycad-like Bennettitales which flourished in the Cretaceous. The foliar trace here was a single bundle—either the primitive single strand, perhaps comparable to that of *Medullosa*, or a fusion of two—which developed in the petiole and blade into a series of typically exarch bundles with centrifugal secondary wood. The reproductive organs were very specialized, and the group has probably given rise to no living family of plants.

The modern Cycadales perhaps constitute a fourth line from the palaeozoic plexus which, however, lies very close to that of the Bennettitales. They have often been considered as derived from forms related to the Lyginodendreae, but the exarch structure of the leaf bundles and the construction of the seed, which is much more comparable to that of *Medullosa* than to that of *Lyginodendron*, make it very improbable that the latter genus has given rise to the modern family. The cycads are also separated from the Bennettitales by the possession of a double leaf trace and a simple reproductive system. The parallel venation of the leaf suggests the Cordaitales, and, as we have remarked above, *Nilssonia* shows an intermediate condition between the two types of leaf.

It seems probable that the group arose in the late Carboniferous from cycad-ferns possessing a double exarch leaf trace and petiolar bundle, a type of leaf intermediate between the ordinary fern frond and the parallel veined cordaitean condition, and a seed resembling that of *Medullosa*.

There are thus apparently two main groups in the exarch series, one of which has progressed toward the coniferous type, and is represented by the Cordaitales and the modern Coniferales, and the other of which has produced the cycadean type, as represented by the Bennettitales and the modern Cycadales.

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EXPLANATION OF PLATE XVII

FIG. 1.—Petiolar bundle of *Cycas revoluta*, showing the typical cycadean condition, with primary and secondary phloem, primary centripetal xylem, and secondary centrifugal xylem; ×150.

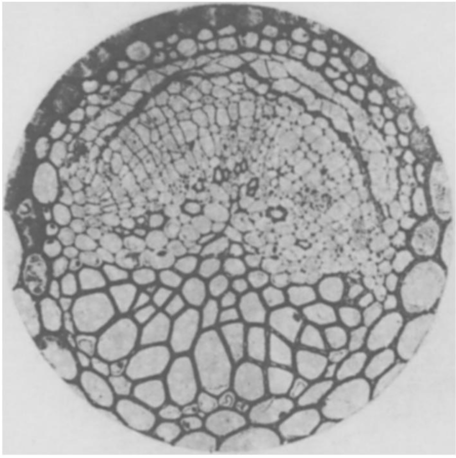
FIG. 2.—Typical petiolar bundle of *Encephalartos Lehmanii*, showing complete absence of centrifugal wood; ×250.

FIG. 3.—Petiolar system of *Zamia Loddegesii*, showing the small amount of centrifugal wood and its radial arrangement.

FIG. 4.—Longitudinal section of a bundle of *Cycas revoluta*, with centrifugal wood on the left and centripetal wood on the right; the protoxylem is clearly in seriation with the latter; ×100.

FIG. 5.—Bundle from the base of the petiole of *Zamia macrophylla*, showing the protoxylem attached to both centrifugal and centripetal wood; ×120.

FIG. 6.—Leaf trace of *Lyginodendron* at its separation from the stele, showing the diarch condition; ×40.



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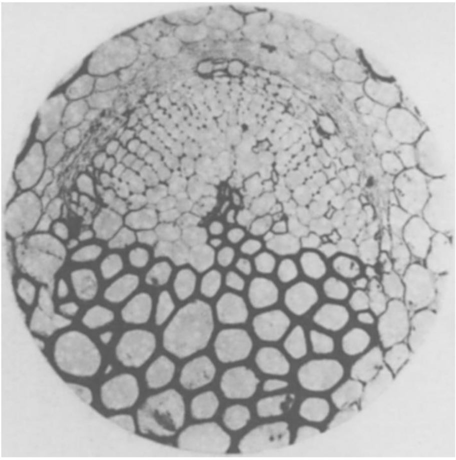

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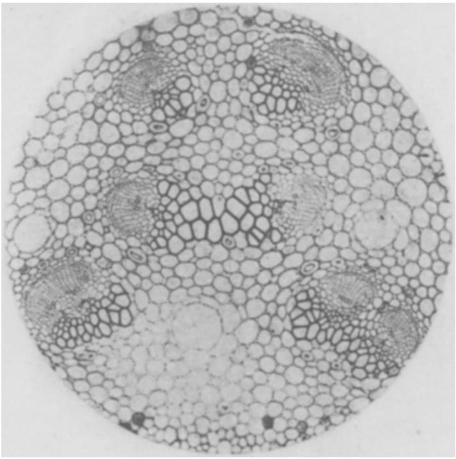

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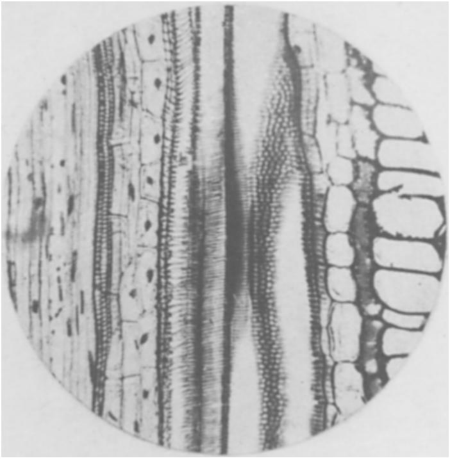

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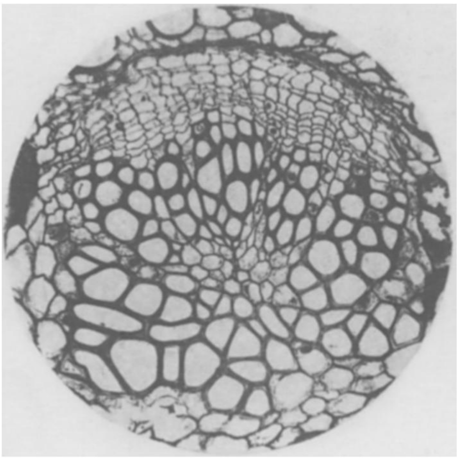

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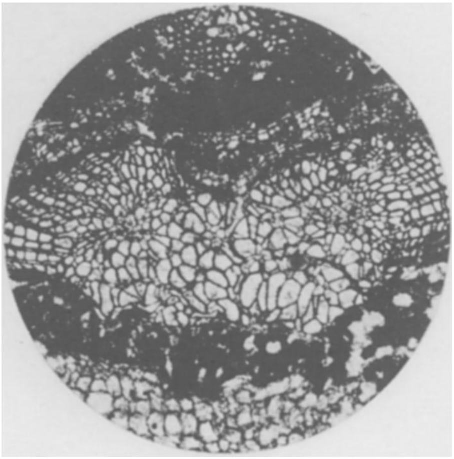

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SINNOTT on FOLIAR BUNDLE